

FINE STRUCTURE OF THE EGGS OF *PSOROPHORA COLUMBIAE*,
PS. CINGULATA AND *PS. FEROX* (DIPTERA: CULICIDAE)

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Abstract.—The eggs of *Psorophora columbiae*, *Ps. cingulata* and *Ps. ferox* are described with reference to scanning electron micrographs. In contrast to earlier descriptions, complete details of the *Ps. columbiae* and *Ps. ferox* eggs are given, including the anterior end and micropyle, posterior end, and intact outer chorion. This is the first account of the egg of *Ps. cingulata*. Eggs of *Ps. ferox* from Florida are discernibly different from a Trinidad population in terms of the number and form of the small outer chorionic tubercles in each chorionic cell.

Key Words: Insecta, mosquito, egg, fine structure, chorionic structure

The known distribution of *Psorophora* (*Grabhamia*) *cingulata* (Fab.) extends through Trinidad, possibly Central America and much of South America (Knight and Stone 1977). It is a species about which little is known, except for a number of records of the larval habitat (Heinemann et al. 1980). Its egg is described here for the first time.

Psorophora (*Janthinosoma*) *ferox* (von Humboldt) is a very widespread species, ranging from South through Central America, the Greater and Lesser Antilles, the eastern United States and south-eastern Canada. The egg of this species was first described by Horsfall et al. (1952), from eggs stripped of the outer chorion. Subsequently, using eggs prepared in the same way, Horsfall et al. (1970) published scanning electron micrographs showing the inner chorionic sculpturing. Although eggs lacking the outer chorion are adequate to demonstrate the basic outline pattern of the outer chorionic cells, the entire structural detail of the outer chorion is lost. In this paper we provide the first description of the intact egg, including

details of the posterior end and anterior end and micropyle. The description is based on eggs from *Ps. ferox* collected in Florida, but we also describe and illustrate differences in eggs from a Trinidad population.

In their papers cited above, Horsfall and associates described (as *Ps. confinnis*) the egg of *Ps.* (*Grabhamia*) *columbiae* (Dyar and Knab). Their material was collected from the eastern United States, which would imply that it is *Ps. columbiae* as currently recognized (Belkin et al. 1970, Darsie and Ward 1981). Bosworth et al. (1983) examined *Ps. columbiae* eggs in more detail as part of their study of eggs of the *Ps. confinnis* complex from 7 areas of the country. However, as in the work by Horsfall and co-workers, the outer chorion was first removed, then the sculpturing of the inner chorion in the anterolateral part of the egg was compared by scanning electron microscopy (SEM). None of these studies, therefore, has presented a description of the egg in its natural form (outer chorion intact), or of all its parts. Following the more complete account in this

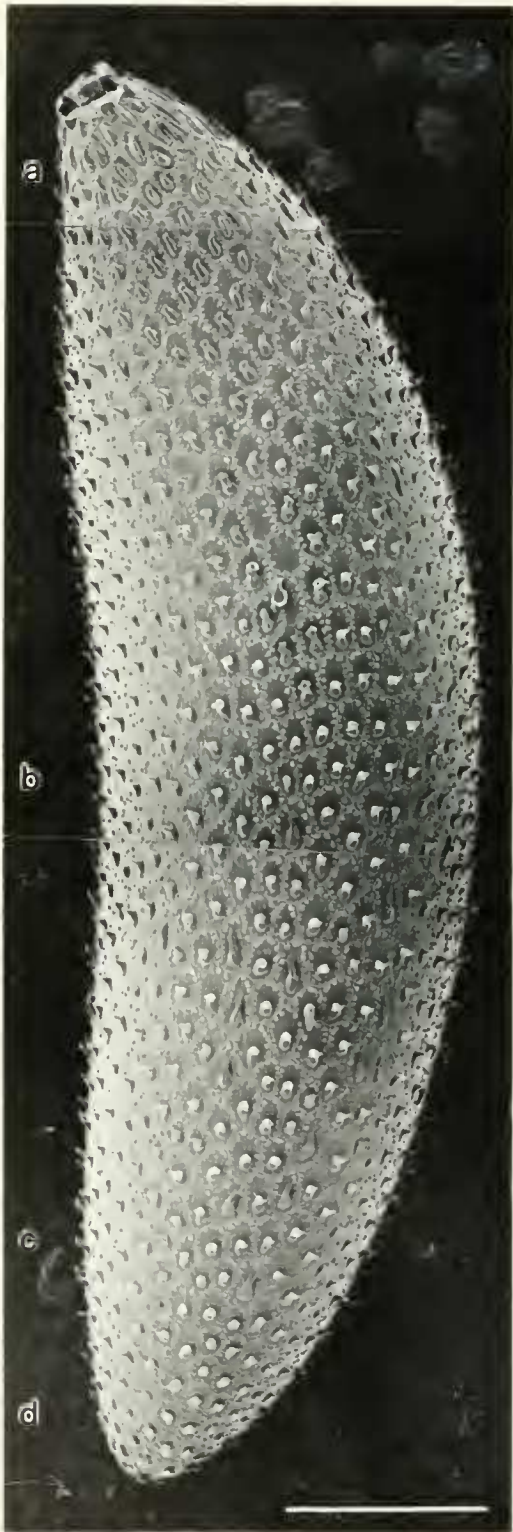


Fig. 1. *Ps. columbiae*. Entire egg, anterior end up-
permost. Scale = 100 μ m.

paper, we point out some characters of the intact egg that may be of value in evaluating a species complex.

MATERIALS AND METHODS

Eggs of *Ps. cingulata* and of *Ps. ferox* were obtained from females collected in the vicinity of Arena, Trinidad, blood-fed and then induced to oviposit in the laboratory. Eggs were allowed to embryonate and were then preserved in 30% ethanol, pre-filtered through a 0.45 μ m polycarbonate membrane, and sent to Vero Beach. On arrival, the eggs were pipetted onto small circles of filter paper and air-dried.

Psorophora ferox eggs from Vero Beach were obtained from females collected on the grounds of the Florida Medical Entomology Laboratory. Eggs of *Ps. columbiae* were from a small laboratory colony established from material collected within a few miles of Vero Beach. When fully embryonated, eggs of both species were suspended in cold, filtered water long enough to pipette them onto circles of filter paper, where they were air-dried. For all three species the paper circles were then attached to stubs with silver paint, completely desiccated over calcium chloride, then coated with gold. Specimens were examined in a Hitachi S-510 SEM.

Measurements of living eggs were done with a stereomicroscope and ocular micrometer. Dimensions and ranges of structures on the egg surfaces were determined from inspection of 5 eggs in each case. The terminology follows Harbach and Knight (1980), except for the terms "anterior ring" and "outer chorionic cell field," defined by Linley (1989).

RESULTS

Psorophora (Grabhamia) columbiae (Figs. 1-3)

Size: dimensions as in Table 1.

Color: dull black.

Overall appearance: broadly banana-shaped, dorsal curvature greater than ventral, widest at about anterior $\frac{1}{3}$, posterior portion gradually tapered, anterior taper

Table 1. Dimensions of eggs of three species of *Psorophora* (n = 10).

Species	Length μm		Width μm		L/W ratio	
	Mean \pm SE	Range	Mean \pm SE	Range	Mean \pm SE	Range
<i>Ps. columbiae</i>	860.9 \pm 17.8	736.4–936.4	235.5 \pm 3.4	218.2–254.5	3.66 \pm 0.05	3.24–3.81
<i>Ps. cingulata</i>	762.1 \pm 1.8	749.9–766.6	240.1 \pm 1.8	233.3–249.9	3.18 \pm 0.03	2.99–3.29
<i>Ps. ferox</i> (Fl)	904.5 \pm 13.7	845.5–963.6	250.2 \pm 3.6	227.9–265.5	3.62 \pm 0.03	3.44–3.75
<i>Ps. ferox</i> (Tr.)	918.3 \pm 1.9	911.0–927.7	316.7 \pm 1.7	311.1–322.2	2.90 \pm 0.02	2.83–3.04

more abrupt and pointed, overall surface appearing spiny, micropylar collar distinct (Fig. 1). Outer chorionic cells longitudinally elongated, each with many small peripheral tubercles and a single large, elongate, anteriorly inclined tubercle (Fig. 1).

Chorion, dorsal, lateral and ventral surfaces: all surfaces very similar (Fig. 1). Chorionic cell structure typified by mid-lateral cells, middle of egg, as follows. Shape mostly hexagonal, occasionally pentagonal, outlines quite variable (Fig. 2e), length 17–26 μm , width 11–18 μm . Cell fields about 2 μm smaller in each dimension. Each cell with a single, large, elongate, anteriorly inclined tubercle, positioned towards posterior part of cell, and a variable number of small tubercles around cell periphery (Figs. 2e, 3e; Table 2). Size distribution (largest diameter) of small tubercles bimodal (Fig. 4), size increase highly significant from posterior to anterior part of cell (Fig. 5). Each large tubercle consisting of a distinct base, upper part of tubercle smooth (but see variations, below), often inclined upward only in anterior $\frac{1}{2}$, length 7–12 μm , width 3–5 μm . Cell floor covered with tiny, more or less round tubercles (Fig. 3e), diameter 0.1–0.2 μm , fewer posterior to large tubercle. Small tubercles tending to be oval, with flared base and distinct upper portion, entire tubercle slightly elongated in same axis as adjacent outer chorionic reticulum (Fig. 3e, f). Chorionic reticulum a fine meshwork, width 1.9–2.7 μm , with central line of closely spaced or fused bead-like protuberances, diameter 0.3–0.6 μm (Fig. 3f).

Outer chorionic cell structure differs from anterior to posterior part of egg. Outer chorionic cells close to anterior end smaller,

length 16–21 μm , width 9–13 μm , large tubercles flat or not as erect, often pointed, with rough upper surfaces (Fig. 3a), small tubercles more irregular. At middle of egg large tubercles more tongue-shaped, almost always erect, smooth, small tubercles more regular (Fig. 3b). Approaching posterior end chorionic cells smaller, length 15–19 μm , width 13–19 μm , large tubercles smaller (Fig. 3c). Cells very close to posterior end even smaller, large tubercles much shorter, cap-like, small tubercles fewer (Fig. 3d).

Anterior end, micropyle: outer chorionic cells as described (Fig. 3a), anterior ring present, diameter 41–44 μm , width 3–9 μm , outer margin with anteriorly curved points (Fig. 2a). Micropylar collar very distinct, almost always complete (no gaps), flared anteriorly (Fig. 2a), height 11–12 μm , outer diameter about 26 μm , outer margin irregular (Fig. 2b, c), wall width variable, 1.5–8 μm , inner diameter about 14 μm , inner edge slightly irregular (Fig. 2c). No micropylar disc visible, micropyle diameter about 2.5 μm .

Posterior end: outer chorionic cells close to end as described (Fig. 3d), end rounded, large tubercles in cells button-like (Fig. 2d).

Psorophora (*Grabhamia*) *cingulata*
(Figs. 6–8)

Size: dimensions as in Table 1.

Color: dull black.

Overall appearance: broadly cigar-shaped, dorsal curvature greater than ventral, anterior end somewhat conical, posterior more rounded, surface somewhat spiny but less so than *Ps. columbiae*, micropylar collar sometimes fairly distinct (Fig. 6), but often not so (Fig. 7a). Outer chorionic cells as in

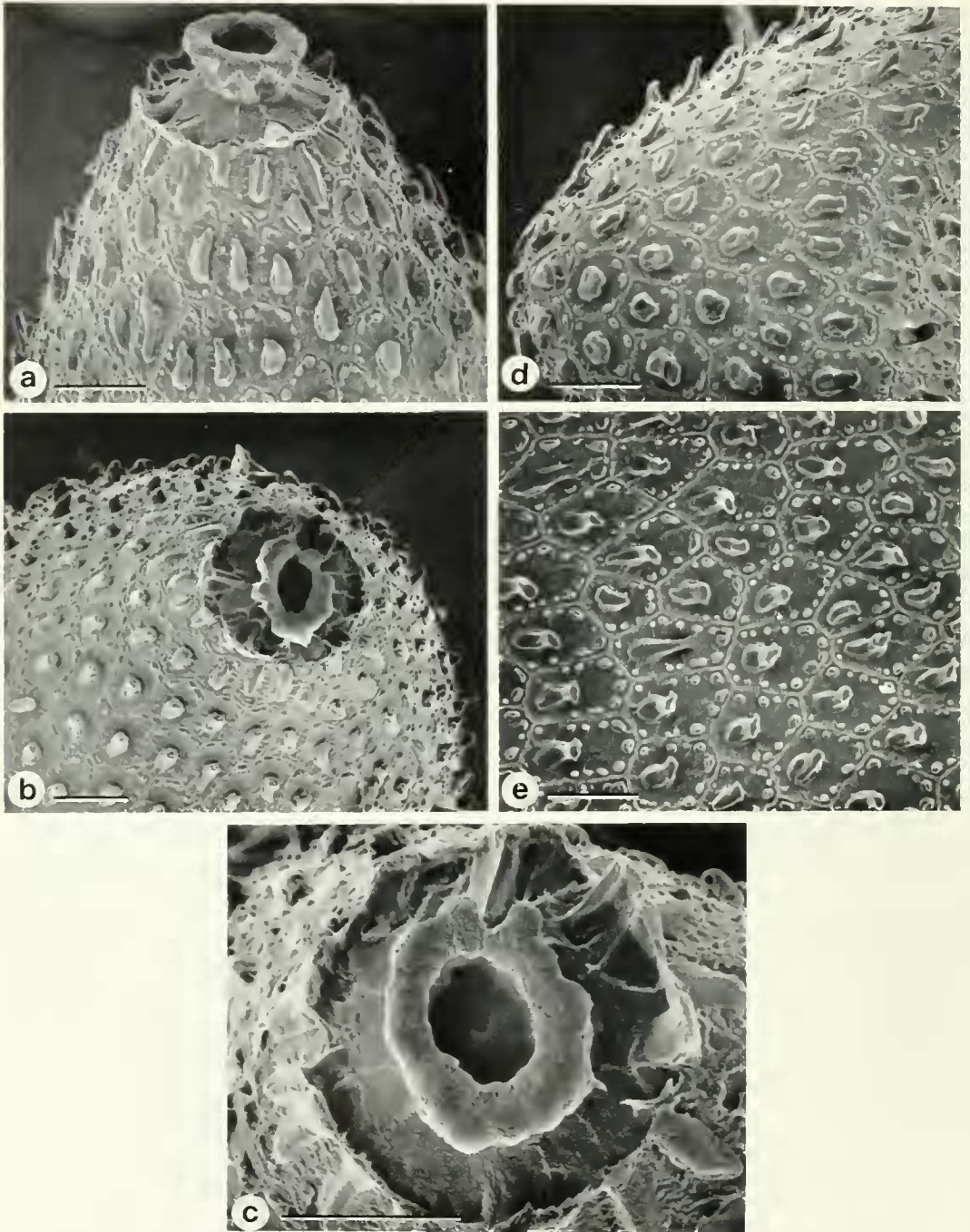


Fig. 2. *Ps. columbiae*. (a) anterior end, dorsal surface; (b) anterior end and micropylar apparatus; (c) detail of micropylar apparatus; (d) posterior end, lateral view; (e) typical outer chorionic cells, lateral surface, middle of egg. Scale = 20 μ m.

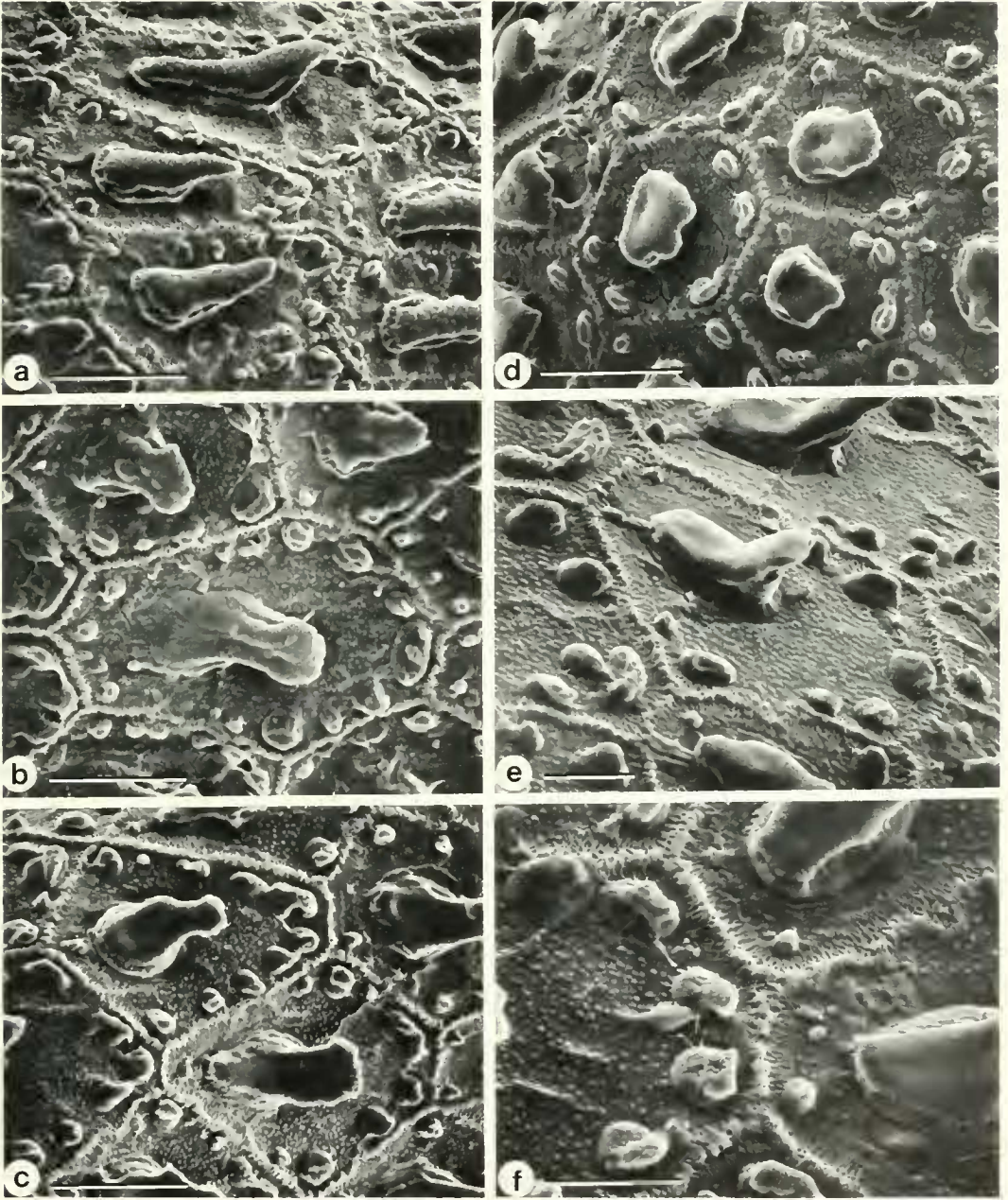


Fig. 3. *Ps. columbiae*, details of lateral outer chorionic cells on different parts of egg (figure letters correspond to positions labelled in Fig. 1). (a) close to anterior end; (b) at about anterior $\frac{1}{3}$; (c) at about posterior $\frac{1}{3}$; (d) very close to posterior end; (e) detail of whole cell, middle of egg; (f) detail of outer chorionic reticulum, middle of egg. Scale = 10 μm (a, b, c, d, e), = 5 μm (f).

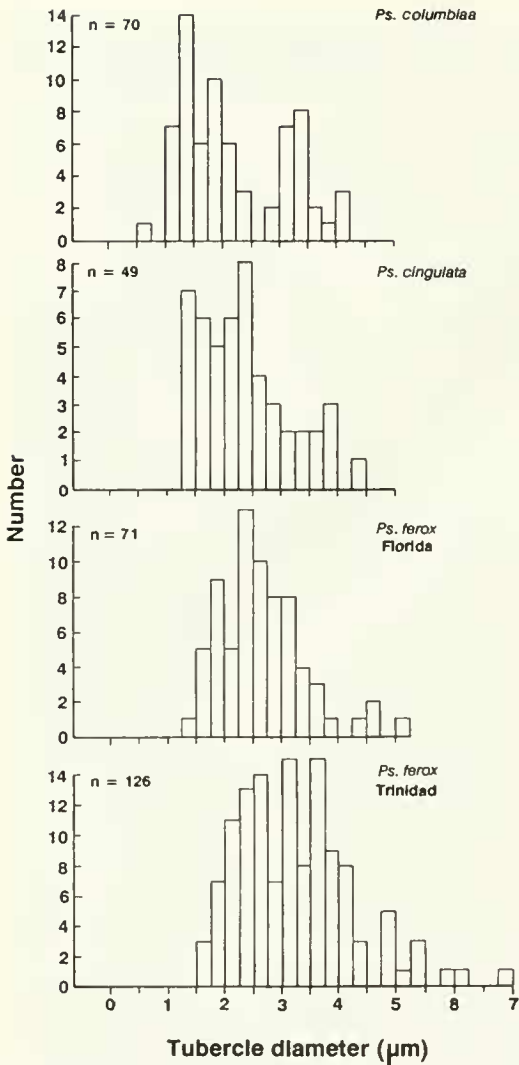


Fig. 4. Size distributions of small outer chorionic tubercles.

Ps. columbiae except that small, peripheral tubercles more numerous (Table 2) and large tubercle sometimes anteriorly inclined, sometimes decumbent (Fig. 6).

Chorion, dorsal, lateral and ventral surfaces: all surfaces very similar (Fig. 6). Outer chorionic cells usually hexagonal, occasionally pentagonal, outlines variable (Fig. 7e), length 25–43 μm , width 21–25 μm . Cell fields about 2 μm smaller in each dimension. Sin-

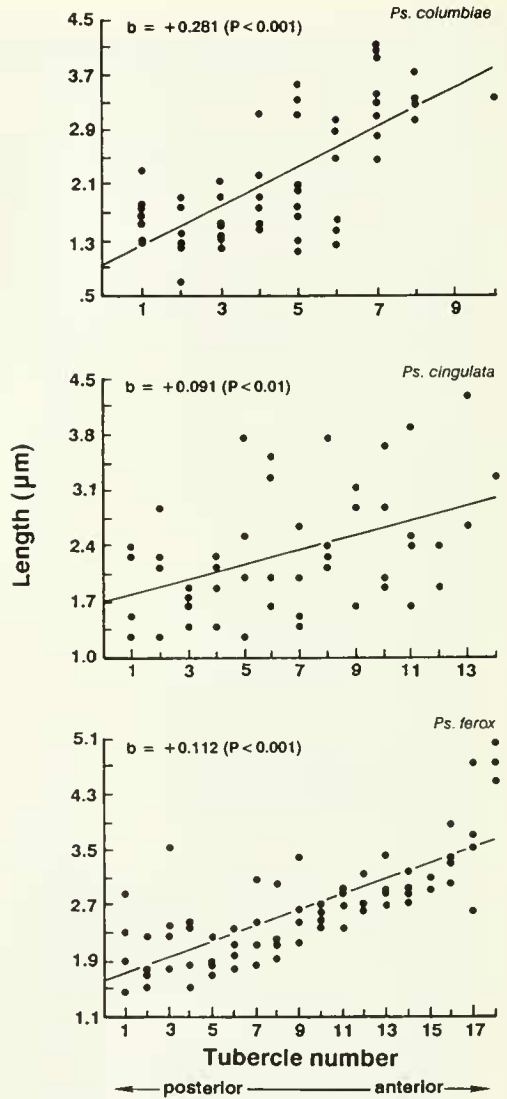


Fig. 5. Regressions of small tubercle length (largest dimension) on position in outer chorionic cell (number of tubercle indicates its numerical position relative to posterior cell boundary).

gle large tubercle positioned well towards posterior part of cell, often inclined anteriorly, but often flat, owing to attachment to cell floor at anterior end (Fig. 7e). Small tubercles variable in number (Table 2), size distribution (largest diameter) skewed (Fig. 4), size increasing significantly from poste-

Table 2. Numbers of small outer chorionic tubercles in three species of *Psorophora*.

Species	n	Number of small tubercles*	
		Mean \pm SE	Range
<i>Ps. columbiae</i>	49	11.9 \pm 0.3	7-16
<i>Ps. cingulata</i>	31	25.0 \pm 0.4	20-29
<i>Ps. ferox</i> (FL)	36	32.9 \pm 1.7	17-51
<i>Ps. ferox</i> (Tr.)	28	27.5 \pm 0.6	23-35

* In outer chorionic cells, mid-lateral surface, middle of egg.

rior to anterior part of cell, but this progression not as great as in *Ps. columbiae* (Fig. 5) and not easily discerned in individual cells (Figs. 7e, 8b). Base of attachment of large tubercle fairly small, upper surface (Fig. 8e) fissured at base, at anterior end, and around edge, smoother centrally (but see variations, below), length 8-18 μ m, width 5-7 μ m. Cell floor with many tiny, round tubercles (Fig. 8e), diameter 0.1-0.5 μ m. Small peripheral tubercles irregular in shape, longest dimension tending to parallel adjacent chorionic reticulum (Fig. 8b), each tubercle having a flared base and distinct upper portion, surfaces smooth (Fig. 8e, f). Outer chorionic reticulum a fine meshwork, only slightly raised, width 0.7-1.5 μ m, with central line of closely spaced or intermittently fused bead-like protuberances, diameter 0.3-0.4 μ m (Fig. 8f).

Variations in outer chorionic cell structure as follows. Cells close to anterior end smaller, length 22-28 μ m, width 12-16 μ m, large tubercles usually flat or very little erect (Figs. 7a, 8a), more pointed, length 8-17 μ m, width 4.5-6.5 μ m, upper surfaces entirely rough (Fig. 8a). Small tubercles more irregular. Approaching posterior end outer chorionic cells become somewhat smaller, length 21-35 μ m, width 17-20 μ m. Large tubercles longer (9-21 μ m), almost always decumbent (Fig. 7d), attached anteriorly to cell floor, often by ragged, finger-like extensions (Figs. 7d, 8c), surfaces smooth except for anterior edges (Fig. 8c). Immediately at

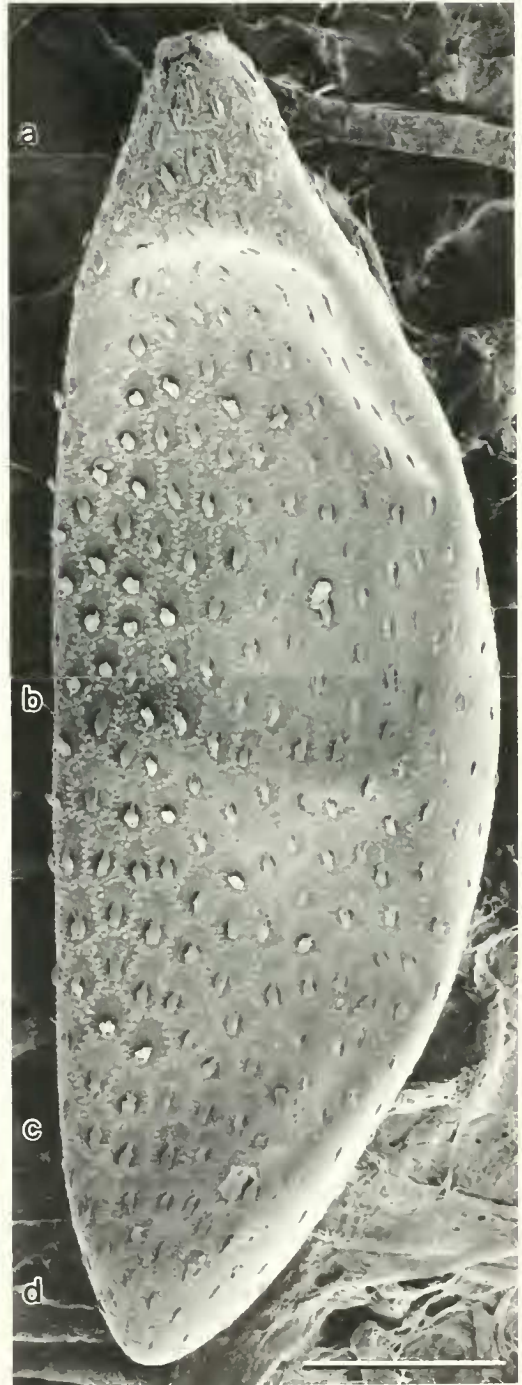


Fig. 6. *Ps. cingulata*. Entire egg, anterior end uppermost. Scale = 100 μ m.

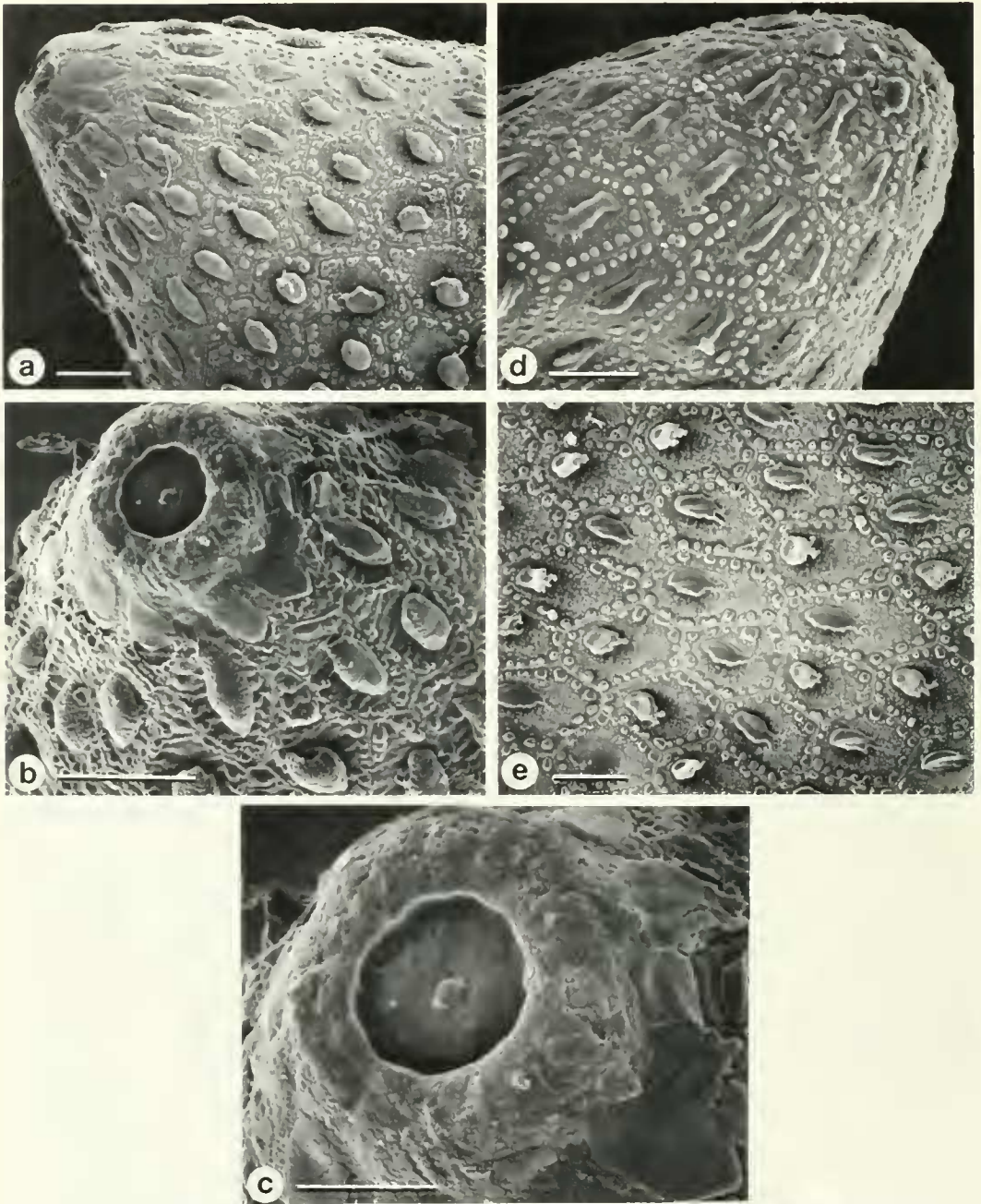


Fig. 7. *Ps. cingulata*. (a) anterior end, dorsal surface; (b) anterior end and micropylar apparatus; (c) detail of micropylar apparatus; (d) posterior end, lateral view; (e) typical outer chorionic cells, lateral surface, middle of egg. Scale = 20 μm (a, b, d, e), = 10 μm (c).

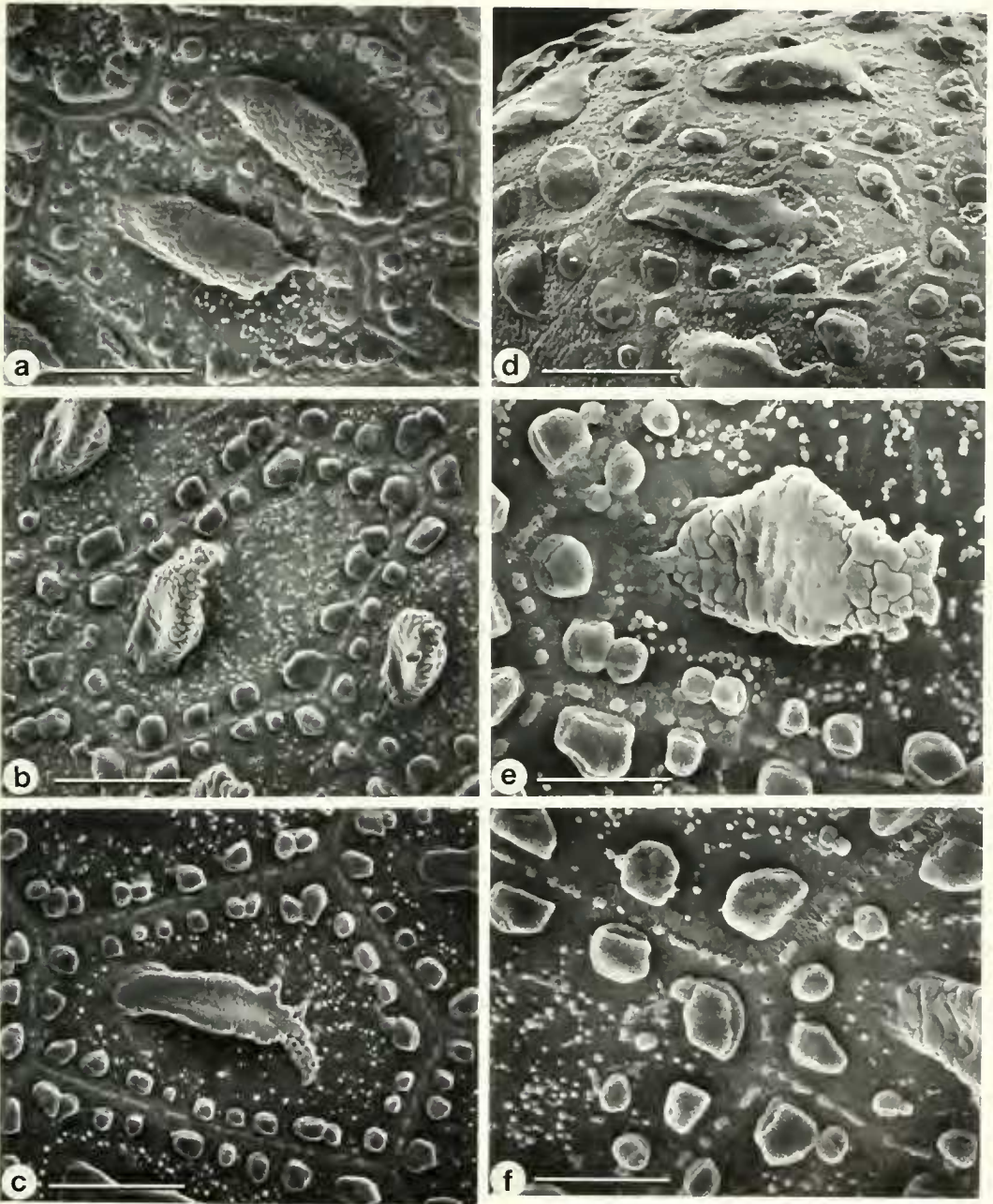


Fig. 8. *Ps. cingulata*, details of lateral outer chorionic cells on different parts of egg (figure letters correspond to positions labelled in Fig. 6). (a) very close to anterior end; (b) at about anterior 1/3; (c) at about posterior 1/3; (d) very close to posterior end; (e) detail of whole cell, middle of egg; (f) detail of outer chorionic reticulum, middle of egg. Scale = 10 μm (a, b, c, d), = 5 μm (e, f).

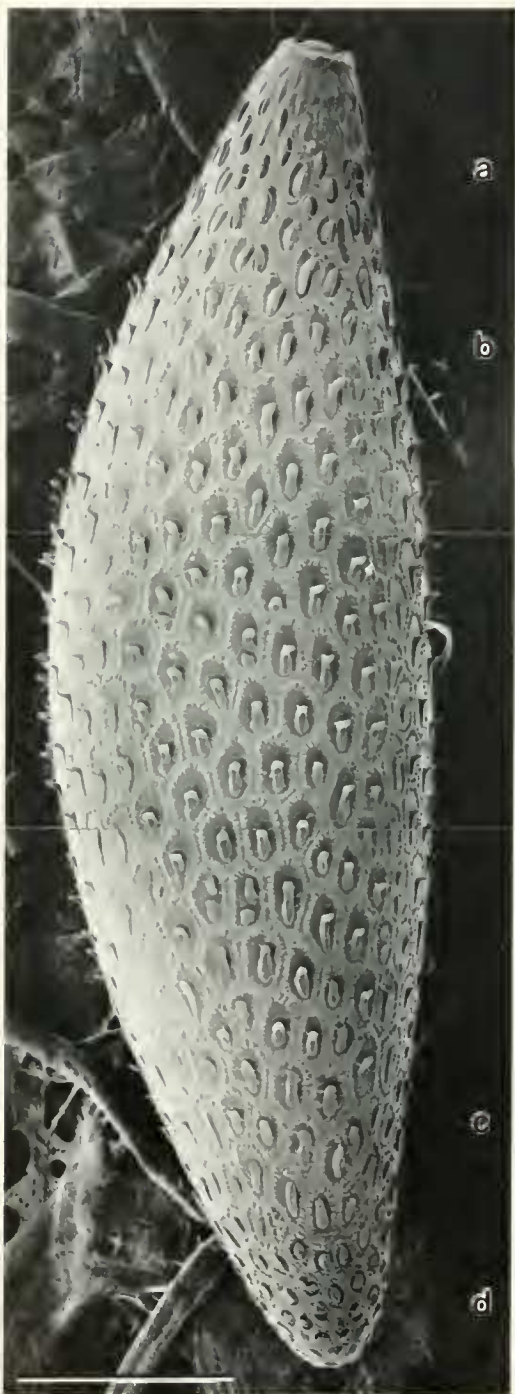


Fig. 9. *Ps. ferox*. Entire egg, anterior end uppermost. Scale = 100 μm .

posterior end large tubercles become scale-like, appressed to cell floors, anterior margins ragged, surfaces smooth (Fig. 8d). Small tubercles few in number.

Anterior end, micropyle: outer chorionic cells as described (Figs. 7a, 8a). Anterior ring absent. Micropylar collar sometimes fairly distinct (Fig. 6), but usually not so (Fig. 7a), complete, height 8–10 μm , usually tapered, outer diameter about 27 μm , outer margin quite regular, but surface rough (Fig. 7b, c), wall width fairly uniform, 5.2–7 μm , inner collar diameter about 13 μm , inner edge formed of a ring of very shallow excavations (Fig. 7b, c). Micropylar disc not clearly visible, micropyle diameter about 2.2 μm .

Posterior end: outer chorionic cells as described, pole rounded, large tubercles in cells capping end button-like (Fig. 7d).

Psorophora (Janthinosoma) ferox
(Figs. 9–11)

Size: dimensions as in Table 1.

Color: black.

Overall appearance: shape somewhat to quite fusiform, dorsal curvature greater than ventral, width greatest just anterior to middle, anterior end especially conical, surface spiny, micropylar collar rather inconspicuous (Fig. 9). Outer chorionic cells distinct, longitudinally elongated, with many peripheral small tubercles and one long, anteriorly inclined one (Fig. 9).

Chorion, dorsal, lateral and ventral surfaces: all surfaces very similar (Fig. 9). Chorionic cells almost always hexagonal, occasionally pentagonal (Fig. 10e), quite uniform in shape (Fig. 8), length 27–43 μm , width 17–24 μm . Cell fields about 2 μm less in each dimension. Each cell with single very long, tongue-like tubercle originating very close to posterior margin of cell field and extending to about anterior $\frac{1}{3}$ (Fig. 10e), tubercle much more sharply inclined from about anterior $\frac{1}{3}$ (Fig. 10e). Small peripheral tubercles numerous (Figs. 10e, 11b, e)

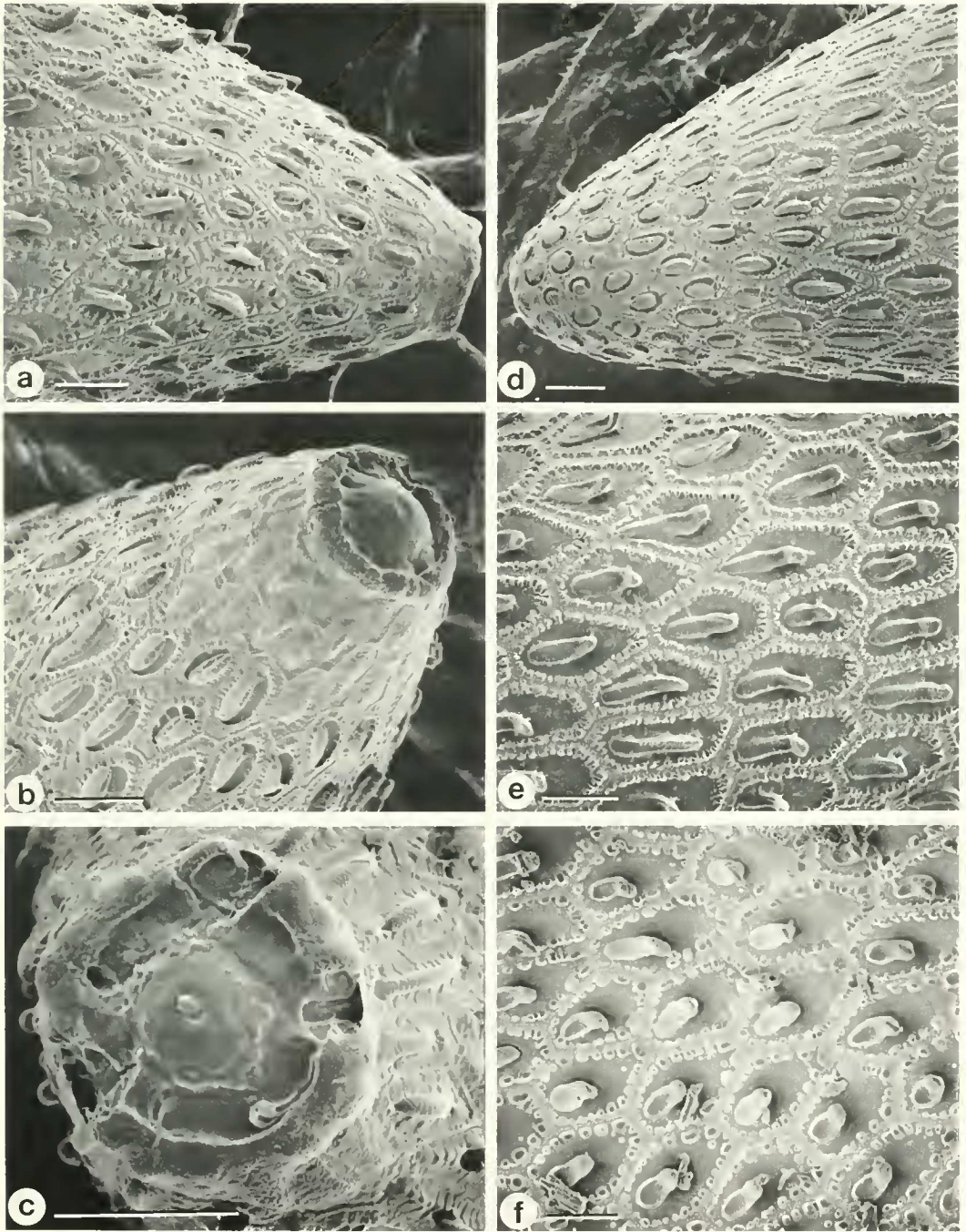


Fig. 10. *Ps. ferox*. (a) anterior end, lateral surface; (b) anterior end and micropylar apparatus; (c) detail of micropylar apparatus; (d) posterior end, lateral view; (e) typical outer chorionic cells (Florida), lateral surface, middle of egg; (f) typical outer chorionic cells (Trinidad), lateral surface, middle of egg. Scale = 20 μ m.

and numbers variable (Table 2), longest dimension usually perpendicular to adjacent chorionic reticulum, size distribution skewed (Fig. 4), and size increasing highly significantly from posterior to anterior part of cell (Fig. 5), as easily visible (Fig. 10e). In detail, large tubercles made up of distinct, flared base, with rough sides (Fig. 11e), supporting tongue-shaped upper portion. Length of tubercle 13–25 μm , width 5.5–7 μm , surface covered with irregular bumps, slightly more defined anteriorly, less so posteriorly (Fig. 11e). Cell floor covered with many tiny tubercles (Fig. 11e, f), diameter 0.1–0.4 μm , tending to be more numerous anteriorly. Small tubercles irregular, but usually tending to be rectangular (Fig. 11b, f), with widely flared base and small, cap-like upper portion, surfaces smooth (Fig. 11f). Chorionic reticulum an intricate, fine meshwork, slightly raised, width 1.1–2.2 μm , with a double, centrally positioned row of small protuberances, diameter 0.1–0.4 μm (Fig. 11e, f). Meshwork of reticulum often extending up outer sides of small tubercles (Fig. 11f).

Structural differences in chorionic cells as follows. Close to anterior end cells considerably smaller, length 16–24 μm , width 9–14 μm . Cell fields become progressively smaller (Fig. 10a, b) until only partially open, usually along one side of large tubercle (Fig. 11b). Inner margins of small tubercles eventually fuse with large tubercle, forming continuous layer (Figs. 10a, b, 11a). Large tubercles not as steeply inclined, becoming more decumbent (Fig. 10a), small tubercles becoming lower anteriorly, shape more irregular, bases flatter, caps often with bumpy surfaces (Fig. 11a). Immediately behind anterior end small tubercles almost disappear (Figs. 10b, 11a), large tubercles appearing as low humps on cell surface (Fig. 10b). Meshwork of chorionic reticulum not distinct, the two central rows of small protuberances closer, forming prominent ridge (Fig. 11a). Somewhat further from anterior end cells much more as in middle of egg,

but large tubercles not as steeply inclined (Fig. 11b), meshwork of reticulum visible but not as distinct, and its two central rows not as widely separated. Towards posterior end, progressive changes are similar to those at anterior end (Figs. 9, 10d). Cells become smaller, small tubercles flatter, large tubercles completely decumbent (Figs. 10d, 11c). Cells at posterior end have partially or almost completely occluded fields, very indistinct or almost indistinguishable small tubercles, and reticulum with meshwork scarcely detectable and pronounced central ridge (Fig. 11d). Large tubercles button-like with surface sculpturing less distinct (Figs. 10d, 11d) and almost invisible on most posterior ones (Fig. 11d).

Anterior end, micropyle: chorionic cells as described. Anterior ring absent, micropylar collar visible but not prominent (Fig. 10a, b), not complete (gaps present), height 7 μm , outer diameter about 40 μm , outer margin bumpy (Fig. 10b, c), wall width variable, 0–6 μm , inner collar diameter about 27 μm , inner margin quite smooth, with very shallow excavations (Fig. 10b, c). Micropylar disc very prominently domed (Fig. 10b, c), diameter about 14 μm , micropyle diameter about 2 μm .

Posterior end: outer chorionic cells as described, rather conical, tapering, and end smoothly rounded (Fig. 10d).

Examination of eggs of *Ps. ferox* from Trinidad revealed a number of distinct differences from the Florida population. Although Trinidad eggs were longer (Table 1), they were not significantly so (*t*-test). They were, however, significantly greater in width ($P < 0.001$), and the length/width ratio consequently was smaller ($P < 0.001$). The outer chorionic cells were similar in outline appearance, but differences in the small peripheral tubercles rendered the Trinidad eggs visually distinct (Fig. 10f cf. 10e). The mean number of tubercles per cell in Trinidad eggs was significantly ($P < 0.01$) smaller (Table 2), and their size, on average, clearly greater (Fig. 4). Normalization by logarithmic

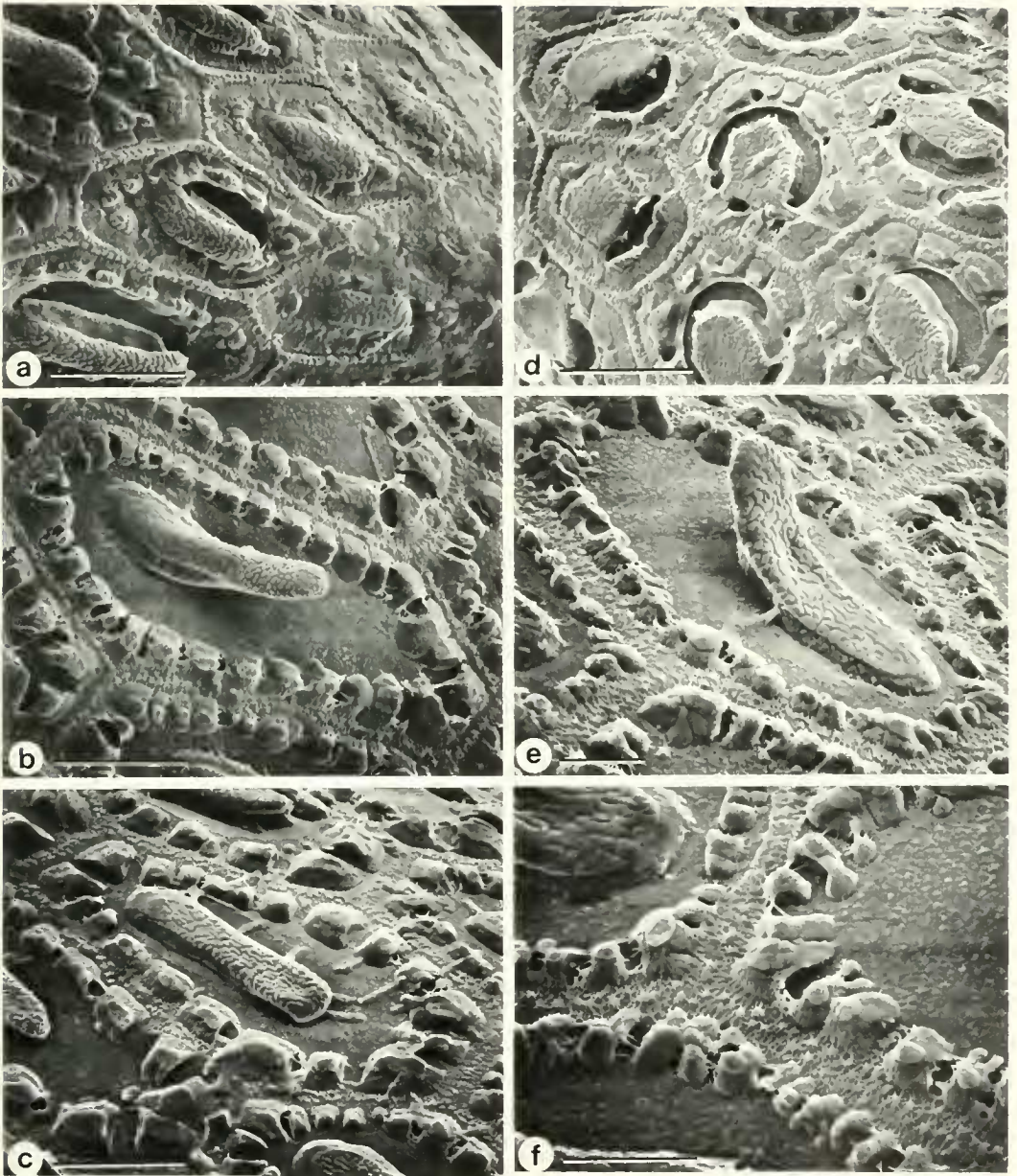


Fig. 11. *Ps. ferox*, details of lateral outer chorionic cells on different parts of egg (figure letters correspond to positions labelled in Fig. 9). (a) very close to anterior end; (b) at about interior $\frac{1}{3}$; (c) at about posterior $\frac{1}{3}$; (d) very close to posterior end; (e) detail of whole cell, middle of egg; (f) detail of outer chorionic reticulum, middle of egg. Scale = $10\ \mu\text{m}$ (a, b, c, d), = $5\ \mu\text{m}$ (e, f).

transformation of the size distributions indeed proved the tubercles of Trinidad eggs to be larger ($P < 0.001$), as easily discernible in the micrographs (Fig. 10f cf. 10e). In ad-

dition to this difference in terms of their largest dimension, the shape of the small tubercles also was different. Thirty tubercles (10 randomly picked from each of 3 eggs

for each population) were measured to record their radial (relative to the cell) and circumferential diameters and the ratios (r/c) calculated. The mean (\pm SE) Trinidad ratio (1.02 ± 0.03) was significantly ($P < 0.001$) smaller than the Florida sample (1.53 ± 0.06), implying a much closer approximation to square in the Trinidad eggs (Fig. 10f cf. 10e).

DISCUSSION

In their survey of the morphology of the inner chorion of eggs of the *Ps. confinnis* complex, Bosworth et al. (1983) examined 21 eggs of *Ps. columbiae* from the same location (Indian River County) as the material studied here. Their inner chorionic pattern type B was the most frequent (67%), with types A (5%), D (14%) and G (14%) also present. Type B is generally consistent with the intact eggs we examined. Notches in the cell outline (corresponding to the midline of the outer chorionic reticulum), some with short ridges extending into the cell field, are visible in Fig. 2e. Some cells seen at higher magnification also accord with type B (Fig. 3a, c, f) in that they appear to have short ridges in the cell fields, not connected with the reticulum. Type D as described by Bosworth et al. (1983) is similar to Type B, except that the cells contain a "cellular disc," which obviously represents an impression of the base of the cell's large tubercle on the inner chorion. Why only some cells stripped of the outer chorion show this impression is not clear. It has occurred to us, however, that the presence or absence of an impression could be determined by inconsistencies in preparative technique. These eggs were rolled on sticky tape to remove the outer chorion (Bosworth et al. 1983) and presumably were subjected to at least some pressure. Differences in this pressure could have caused a gradation in the amount of detail impressed onto the inner chorion. Outer chorionic structures are easily removed from these eggs by abrasion. Thus, it is also possible that some or many

of the cells lacked the outer chorionic tubercles when the egg was applied to the sticky tape and could not have left an impression. Admittedly, cell outlines are not likely to be affected by removal of the outer chorion, but the possibility of preparative artifacts suggests the need for caution when interpreting inner chorionic patterns.

Given that egg surfaces are to be examined by SEM, there is nothing to be gained by removing the outer chorion. Aside from possible artifacts, much structure, along with its potential variation, is lost. This is illustrated by *Ps. ferox* eggs from Trinidad and Florida, where the number, greatest diameter and form of the small tubercles were all demonstrably different. The small tubercles were, of course, removed from eggs studied by Bosworth et al. (1983), but there is suggestive evidence that they may differ in number between populations of the *Ps. confinnis* complex. A few of the eggs from Arkansas and Texas possessed an unusual inner chorionic pattern (type J), in which the periphery of each cell was lined with small ovoid pits, almost certainly corresponding to the small tubercles. Bosworth et al. (1983) state that 15–20 pits were present in each cell, apparently more than in *Ps. columbiae* eggs from Florida, where the numbers ranged from 7–16 (mean 11.9) in 49 cells counted. Tubercle numbers are related to cell size, but the anterolateral cells studied by Bosworth and co-workers would tend to be smaller (and therefore have fewer tubercles) than those selected here, which were laterally positioned in the middle of the egg. A re-examination of eggs of the *Ps. confinnis* complex, making use of the intact structural detail of the outer chorion, should be undertaken.

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